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Predator Interference and the Establishment of Generalist Predator Populations for Biocontrol

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We conducted a field experiment to determine the extent to which interference among generalist predators limits their effectiveness as biocontrol agents. We manipulated immigration of a guild of actively hunting generalist ground predators, carabid beetles and lycosid spiders, by intercepting them as they attempted to enter fenced 50-m^2 vegetable gardens. Immigration was blocked, allowed at the mean rate measured at our field site, or doubled. Altered immigration rates were maintained through a spring garden of cabbage, bean, eggplant, and cucumber, followed by a summer garden of squash. We monitored densities of carabids and lycosids to discover if altering their immigration rate changed their densities in the plots. We also measured densities of other predators on the ground and in plant foliage, pest numbers, and vegetable yields. Doubling the immigration rate of carabids and lycosids approximately doubled the densities of carabids inside the plots, but did not increase lycosid densities. Increasing the rate of immigration of carabids and lycosids depressed densities of nonlycosid ground spiders. In the spring gardens, manipulation of carabid and lycosid immigration did not influence numbers of predators or herbivores in the foliage and did not affect vegetable productivity. In contrast, in the summer gardens, foliage-dwelling predators were lower, pest densities were marginally lower, and squash productivity was higher in the carabid and lycosid immigration plots compared to the no-immigration treatment. Doubling carabid and lycosid immigration rate never increased the magnitude of their effects on other predators, pests, or plant productivity. Predator interference limited lycosid establishment, reduced densities of other predator taxa, and apparently prevented a doubling of carabid densities from having an increased impact on pest numbers. Nevertheless, despite widespread effects of predator interference, allowing immigration of lycosids and carabids increased squash productivity. © 1999 Academic Press

Key Words: **biological control; generalist predator; predator–predator interference; cannibalism; intraguild predation; vegetable; carabid beetle; wolf spider; Carabidae; Lycosidae.**

INTRODUCTION

Generalist predators, although abundant in agricultural systems, have generally been thought to be poor biocontrol agents. This prediction is based largely on theoretical considerations (e.g., generalist predators lack prey specificity and often have longer generation times than pests) (Riechert and Lockley, 1984). Also, generalist predators interfere with other predators in addition to preying upon herbivorous pests (Polis and Holt, 1992). We define interference among predators to include intraguild predation (IGP), cannibalism, predator avoidance behavior, and predator–predator competition. The high frequency of interference among predators, coupled with their often long development times, makes mass rearing of generalist predators economically unfeasible (DeBach and Rosen, 1991). Therefore, much research has focused on identifying and manipulating characteristics of surrounding habitats to provide source populations of predators to migrate into agricultural fields (Best *et al.*, 1981; Gravesen and Toft, 1987; Nentwig, 1988; Luff and Rushton, 1989; Mangan and Byers, 1989; Heidger and Nentwig, 1989; Hance *et al.*, 1990; Bedford and Usher, 1994; Kajak and Lukasiewicz, 1994; Barbosa, 1998). However, increasing the rate of predator immigration may not increase field densities if predator interference leads to strong *in situ* self regulation.

Predator interference makes predicting the impact of generalist predators on plant productivity difficult, because they may reduce pests directly while simultaneously enhancing pests indirectly by lessening predation pressure from other natural enemies (Polis and Holt, 1992; Rosenheim *et al.*, 1993, 1995). Despite theoretical misgivings, increasing evidence indicates that generalist predators can reduce pest populations in agroecosystems (e.g., Riechert and Lockley, 1984; Chiverton, 1986; Nyffeler and Benz, 1987; Young and

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Edwards, 1990; Wise, 1993; Rosenheim *et al.*, 1993; Nyffeler *et al.*, 1994a,b; Lang, 1997). The challenge is to reconcile the theoretical limitations of generalist predators as biocontrol agents with their reported effectiveness in some agroecosystems. Is predator interference as common as has been predicted and do these behaviors prevent generalist predators from being effective biocontrol agents? The potential complexity of interpredator interactions makes it difficult to answer these questions without conducting large-scale field experiments (Rosenheim *et al.*, 1995).

Generalist predators of the ground layer, particularly carabid beetles (Coleoptera: Carabidae) and wolf spiders (Araneae: Lycosidae), are abundant in many temperate agroecosystems (Thiele, 1977; Wise, 1993). Carabids and lycosids consume a wide spectrum of crop pests (carabids: Best and Beegle, 1977; Frank, 1971; Sunderland and Vickerman, 1980; Barney and Pass, 1986a; Sunderland *et al.*, 1987; Floate *et al.*, 1990; Hamon *et al.*, 1990; lycosids: Kiritani *et al.*, 1972; Yeargan, 1975; Nyffeler and Benz, 1988; Agnew and Smith, 1989; Hayes and Lockley, 1990; Nyffeler *et al.*, 1994a,b; Lang, 1997). Studies have reported both carabids and lycosids feeding on other predators of both the ground layer and plant foliage (e.g., Yeargan, 1975; Sunderland, 1975; Agnew and Smith, 1989; Hayes and Lockley, 1990; Nyffeler *et al.*, 1994a,b). Furthermore, lycosids and carabids may feed upon one another (Shough, 1940; Sunderland, 1975; Hayes and Lockley, 1990) and cannibalism occurs in species of both taxa (Kirk, 1973; Tomlin, 1975; Thiele, 1977; Wagner and Wise, 1996).

Despite the potential for extensive interference among carabids and wolf spiders, growing evidence suggests that these generalist predators can suppress densities of insect pests. Excluding immigrating carabids with barriers elevates densities of cereal aphids (Edwards *et al.*, 1979; Chiverton, 1986). Field experiments and unreplicated, unintentional reductions of lycosid numbers from pesticide applications demonstrate that lycosid predation depresses leafhopper and planthopper pests of rice (Kiritani and Kakiya, 1975; Oraze and Grigarick, 1989). The few studies that have measured indirect effects of carabids and spiders on plants found decreased leaf damage where carabid or spider densities were increased (Clark *et al.*, 1994; Riechert and Bishop, 1990; Carter and Rypstra, 1995). However, crop plants can often sustain considerable damage before yield is reduced (DeBach and Rosen, 1991). Ultimately, yield is the measure of biocontrol effectiveness of relevance to commercial growers. Thus, it remains unclear whether or not predation by carabids and spiders can have economic benefits.

We conducted a field experiment, and complementary laboratory feeding trials, to address: (1) if predator interference regulates densities of carabids and lycosids; (2) if carabids and lycosids reduce densities of other predators, such as other spiders, predatory hemipterans, etc.; and (3) despite predator interference, if carabids and lycosids can still be effective biocontrol agents. We manipulated densities of carabids and lycosids, the major actively hunting ground predators in our system, by regulating their immigration into replicated, fenced vegetable gardens through two crop cycles. We measured the impact of varied immigration rates on resulting carabid and lycosid densities, on densities of other predators and herbivorous pests, and on vegetable production. To aid in interpretation of the results from the field experiment, we also conducted laboratory feeding studies to determine which carabid and lycosid taxa would feed upon one another, on other ground-layer predators, and on vegetable pests.

METHODS AND MATERIALS

Our field site was a 5.6-ha pasture on the University of Kentucky Spindletop Research Farm in Fayette County, KY. The pasture had been mowed but not grazed or planted in crops for at least 2–3 years. Sixteen 5 × 10-m plots, each separated by 30 m of pasture, were plowed in early May 1996. Fences and traps to regulate immigration were installed immediately after plowing. We manipulated densities of carabids and lycosids in fenced plots by controlling immigration from the surrounding pasture. The low fence barrier allowed control of immigration by ground-active arthropods, but did not prevent colonization of the plots by winged insect pests or winged natural enemies. Three fenced treatments, one replicate in each of four blocks, were established: 0X—carabid and lycosid immigration prevented; 1X—carabids and lycosids caught in traps along the outside of the fences added at the normal immigration rate; 2X—carabids and lycosids added at double the normal immigration rate. Each block also contained an unfenced reference plot (= OPEN), in which immigration was not manipulated, but which was otherwise treated as the fenced plots.

In early June 1996 we transplanted cucumber (*Cucumis sativus* L.), cabbage (*Brassica oleracea* L.), and eggplant (*Solanum melongena* L.), started 4–6 weeks earlier in the greenhouse, and planted beans (*Phaseolus vulgarus* L.) from seed, with one row of each arranged randomly in each plot. Planting techniques and densities followed extension recommendations for central Kentucky (Strang *et al.*, 1994). In late July and early August, crops in the spring gardens were harvested and a second crop, a monoculture of squash (*Cucumis pepo* L.), was planted in all plots.

We selected squash for the summer garden because preliminary data analyses and the biology of pests at our site suggested that carabids and lycosids most

likely would enhance productivity of cucurbits. Cucumber beetles (striped cucumber beetles, *Acalymma vittata* F., and spotted cucumber beetles, *Diabrotica undecimpunctata howardi* Barber, both occur at our site) oviposit in the soil, where larvae feed on plant roots and eventually pupate (Elsey, 1988; Krysan, 1986). As larvae, cucumber beetles are subject to predation by carabids (Brust, 1991). When emerging from pupae and during oviposition, adult cucumber beetles are exposed to predation by both carabids and lycosids. Squash bug (*Anasa tristis* De Geer) adults are more common on the ground surface than on plants through much of the season and deposit egg masses primarily on lower leaves of squash (Palumbo *et al.*, 1991). Also, squash bug adults and nymphs will congregate under mulch cover (Cartwright *et al.*, 1990).

To enhance the survival of ground predators and to retard weed growth, all gardens were covered with 10 cm of straw mulch immediately after the first crops were planted. This depth was maintained with periodic additions of fresh straw. We also hand-pulled weeds occasionally to maintain low weed densities. The plots were not irrigated, fertilized, or treated with pesticides.

The Arthropod Community

Species lists have been published of carabids (Barney and Pass, 1986a,b) and spiders (Culin and Yeargan, 1983a,b) found in agricultural fields in central Kentucky. Carabids are dominated by *Scarites* spp. [at least three species occurred at our site, but are difficult to distinguish in the field (Barney and Pass, 1986b)], *Evarthrus sodalis* LeConte, and *Harpalus pennsylvanicus* De Geer. *Scarites* spp. and *E. sodalis* are primarily predaceous (Barney and Pass, 1986a), but *H. pennsylvanicus* is highly omnivorous, with seeds making up a large fraction of its diet (Barney and Pass, 1986a). In central Kentucky, *Scarites* is most active in May and June, *E. sodalis* is most active in June and July, and *H. pennsylvanicus* activity reaches a peak in July and August (Barney and Pass, 1986b; Snyder and Wise, *pers. obs.*). These three carabid taxa together comprised 60% of the seasonal catch reported by Barney and Pass (1986b). We identified all carabids to species, except *Scarites* spp.

Culin and Yeargan (1983b) reported that *Hogna*, *Rabidosa*, and *Pardosa*, which are active throughout the summer, are the dominant lycosids in our area. The most common lycosid species at our site are *H. helluo* Hentz, *P. milvina* Hentz, and *P. saxitilis* Hentz (Snyder and Wise, *pers. obs.*). *Hogna* and *Pardosa* represented 60% of Culin and Yeargan's lycosid catch. Only adult wolf spiders can reliably be identified to species, and then only by examination of the genitalia. Because this was logistically unfeasible in our experiment, we identified lycosids to genus.

All species of carabid beetles and wolf spiders that we trapped were added to field plots, but only the most abundant taxa of carabid and wolf spider were used in the laboratory feeding trials (described below).

Technique for Regulating Immigration

Natural colonization of the plots by carabids and lycosids was blocked with a 36-cm fence of aluminum flashing, with a 5-cm horizontal lip at the top (see Wagner and Wise, 1996, for fence design). Each fence was lined on the outside with 1-m-long trench traps (Fig. 1A) spaced 1 m apart, with 12 trench traps/plot (Fig. 1B). Traps were checked daily for intercepted arthropods and all captured animals other than carabids and lycosids, including herbivores, were released into the gardens immediately. Ground beetles and wolf spiders were pooled haphazardly and then introduced into the fenced plots at one of three rates: 0X, 1X, or 2X the overall mean rate of capture per plot. The mean capture rate measured the normal rate of immigration into the plots, assuming that carabids and lycosids did not avoid or escape from the traps or prey upon each other to a significant extent while trapped.

A potential problem with this procedure was the possibility of creating higher-than-normal densities within the plots. Two adjustments were made to compensate for the absence of emigration. First, because pitfall traps often disproportionately trap adult male spiders (Topping and Sunderland, 1992), the number of male lycosids added was adjusted to maintain a 1:1 sex ratio. The rate of capture of females was judged low enough to require no further adjustments. Second, because trapping rates were high for the three most abundant

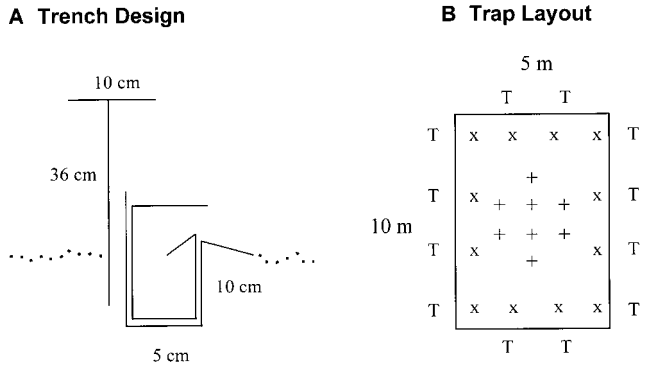

FIG. 1. (A) Cross section of trench trap and fence. Trench traps faced the meadow surrounding each plot. The outer sheath of the trap remained in the ground, but the inner sheath could be lifted out; each end was fitted with a cap which could be removed so that trapped arthropods could be poured into a bucket for initial sorting. Bent lips of inner sheath prevented trapped carabids and lycosids from crawling out of the traps. Each trap was 1 m long. (B) Plots were 5 × 10 m, and fenced plots were lined on the outside with trench traps ("T"). All plots contained eight pitfall traps for censusing carabid and lycosid activity-densities ("+"). 0X plots had additional cup traps ("X") lining the inside of the fence, which were used to capture and remove carabids and lycosids.

carabids (*Scarites* spp., *E. sodalis*, and *H. pennsylvanicus*), and because male and female carabids cannot easily be distinguished by external features, we released no more than 1 individual carabid/species/m^2 within each 2-week release period (double this number for the 2X plots). This target density was based on typical carabid densities in northern temperate agricultural systems (Thiele, 1977). Carabids trapped in excess of this amount were released outside the plots.

We did not expect that blocking immigration into 0X plots would completely reduce carabid and lycosid immigration, because adult carabids could emerge from larvae in the plots, some carabids can fly, and lycosids could balloon over plot fences. Thus, we removed carabids and lycosids from the 0X plots by live trapping with 10 pitfall traps (9 cm diameter $\times$ 16 cm deep) along the inside of the fence (Fig. 1B). These traps were run for 3 days at approximately 2-week intervals. Traps were checked every 12 h. All trapped carabids and lycosids were removed and all other arthropods were released back in the plot. Removal traps were always closed at least 3 days before we estimated carabid and lycosid activity-densities.

Sampling and Statistical Analyses

After releasing immigrating predators for 10 consecutive days, we closed the trench traps and estimated ground predator activity-densities within the plots (including the open reference plots) by running eight live pitfall traps per plot (interior traps only, Fig. 1A) for 3 days. Interior traps were then closed, trench traps were reopened, and manipulation of immigration was resumed. This cycle was followed from June (immediately after first planting) until mid-October (just before squash harvest).

The impact of carabid and lycosid immigration on other predators of the ground layer was measured using a portable suction sampler (D-vac Co., Ventura, CA) to collect arthropods from the straw mulch (Marston *et al.*, 1976; Snyder and Hurd, 1995). For each plot, we sampled four randomly selected 0.45-m^2 areas of mulch. Samples were collected during harvest of the spring garden and early in the summer garden of squash (26 August). The impact of the manipulations on the rest of the arthropod community was assessed by suction sampling of the entire row of each vegetable immediately after harvest.

Vegetable production was measured as fruit yield (kg) per plant.

Treatment effects on seasonal means of carabid and lycosid activity-densities were analyzed by orthogonal planned contrasts: (1) 0X vs pooled immigration plots (the mean of the response in 1X and 2X plots within each block) to test the effect of lycosids and carabids and (2) 1X vs 2X to test the effect of doubling predator immigration.

These planned contrasts were also used for evaluating treatment effects on other predators, herbivores, and vegetable production. Effects on predator and herbivore numbers in the summer garden were analyzed further by comparing treatment effects on pooled seasonal mean densities of the most abundant arthropod species on cucurbits (cucumber and squash). We performed this analysis because cucumbers and squash share pest and predator complexes that were present through the entire season.

Activity-densities of carabids and lycosids, densities of other predators and pests, and plant productivity in 1X and OPEN plots were also compared by ANOVA as a measure of our ability to replicate open-plot field conditions in the fenced plots. This comparison only approximately reflects differences in densities of carabids and lycosids because of differences between fenced and open plots in the effective area sampled by pitfall trapping (Wise, 1981).

Data were log-transformed when necessary to meet the assumptions of ANOVA.

Feeding Trials

Predators collected from our field site were placed together in pairs for 7 days in 30 $\times$ 15 $\times$ 10-cm plastic containers with a 1-cm soil substrate. The soil surface and container sides were sprayed with water after 4 days to maintain humidity.

Predators were paired with another of the same taxon (genus or species), with other carabid and lycosid taxa, and with two other spiders of the ground layer (the crab spider *Xysticus* spp. and web spinners in the family Linyphiidae). After 7 days, dead or missing predators were scored as having been preyed upon by the partner remaining alive. Usually, some remains of the victim were found to verify predation (for example, the elytra of carabids were never fully consumed), although with some small victims, identifiable remains were rarely recovered (e.g., linyphiid spiders).

Using an identical protocol, with the exception that trials were run for only 3 days, we paired the common carabids and lycosids with adults of two cucurbit pests—spotted cucumber beetle (*D. u. howardi*) and striped cucumber beetle (*A. vittata*)—and with eggs and nymphs of a third pest of cucurbits, the squash bug (*A. tristis*).

Predators and pests were also maintained singly as a concurrent control to quantify mortality not attributable to predation.

RESULTS

Carabid and lycosid taxa trapped were consistent with a previously published report for our site (Barney and Pass, 1986b). *Scarites* spp., *E. sodalis*, and *H. pennsylvanicus* were the most abundant carabids, rep-

resenting 10, 14, and 64% of our total catch, respectively. *Hogna* and *Pardosa* were the most abundant lycosid genera, respectively representing 30 and 45% of all wolf spiders trapped.

Our techniques were highly effective in manipulating rates of immigration by both carabids and lycosids, judging by the significantly reduced numbers in the 0X treatment (Figs. 2A and 2B; $F_{1,3} = 128.86$, $P = 0.001$ and $F_{1,3} = 43.78$, $P = 0.004$, for carabids and lycosids, respectively).

Impacts of Carabid and Lycosid Manipulation

Doubling immigration rate produced a twofold increase in carabid activity-densities (Fig. 2A; $F_{1,3} = 8.72$, $P = 0.030$). In contrast, doubling lycosid immigration did not increase activity-densities of wolf spiders (Fig. 2B; $F_{1,3} = 0.04$, $P = 0.424$). Lycosid spiderlings from straw mulch d-vac samples also were not significantly increased by doubling the immigration rate of older stages and adults (Fig. 2C; $F_{1,3} = 0.51$, $P = 0.526$).

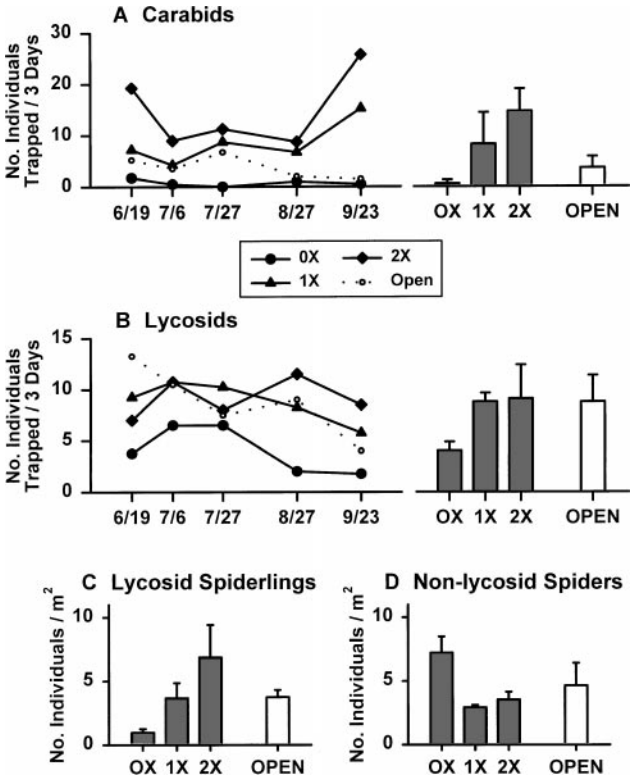

FIG. 2. (A) Seasonal trend and seasonal means of carabid activity-densities inside plots. Treatment codes: 0X, carabid and lycosid immigration blocked; 1X, normal immigration rate; 2X, doubled immigration rate; OPEN, open reference plots. Activity-densities based on pitfall trap catch. (B) Seasonal trend and seasonal means of lycosid activity-densities, based on pitfall trap catch. (C) Lycosid spiderling densities from D-vac samples of straw mulch. (D) Nonlycosid spider densities from straw D-vac samples. No nonlycosid spiders were directly manipulated. Values in this and subsequent figures are means ± SE.

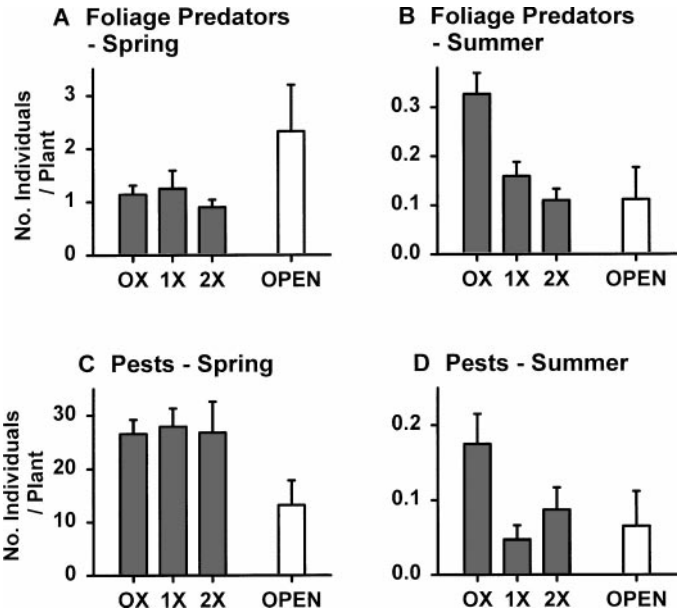

FIG. 3. Densities of foliage predators or herbivorous pests from D-vac samples. The entire row of each vegetable was sampled once, just after harvest. (A) Foliage predators in the spring gardens. (B) Foliage predators in the summer gardens. (C) Herbivorous pests in the spring gardens. (D) Herbivorous pests in the summer gardens.

Carabid and lycosid immigration reduced densities of nonlycosid spiders in straw mulch samples by >50% (Fig. 2D; $F_{1,3} = 53.31$, $P = 0.005$); the magnitude of this reduction did not increase when immigration was doubled (Fig. 2D; $F_{1,3} = 0.55$, $P = 0.512$).

Major foliage predators, in order of descending abundance with scientific name and percentage of total catch in parentheses, were nonlycosid spiders (Araneae, 33%), nabid bugs (*Nabis* spp., 23%), big-eyed bugs (*Geocoris* spp., 16%), and scorpion flies (Mecoptera, 13%). Lacewings, predatory anthocorid bugs, ants, and staphylinid and coccinellid beetles each comprised <5% of the total catch.

In the spring garden, densities of predators in the foliage were not affected by carabids and lycosids (Fig. 3A; $F_{1,3} = 0.08$, $P = 0.799$). However, in the summer garden, foliage predators were significantly lower in pooled 1X and 2X plots compared to 0X plots, although numbers in 1X and 2X did not differ significantly (Fig. 3B; $F_{1,3} = 40.38$, $P = 0.008$).

Pests for each vegetable are given in order of descending abundance, with percentage of total catch in parentheses. On cabbage we found imported cabbage worm, *Artogeia rapae* L. (98%), and cabbage looper, *Trichoplusia ni* Hubner (2%); on bean, striped cucumber beetle (62%), spotted cucumber beetle (32%), and bean leaf beetle, *Cerotoma trifurcata* Forster (6%); on eggplant, flea beetle, *Epitrix* spp. (100%); and on cucumbers, squash bug (65%) and striped (26%) and spotted (9%) cucumber beetles. Herbivore densities were highest on

eggplant (40 ± 10/plant), intermediate on cabbage (9.6 ± 0.6/plant) and cucumber (4.5 ± 1/plant), and lowest on bean (0.40 ± 0.1/m row). Total herbivore densities per plot did not differ between treatments (Fig. 3C; $F_{1,3} = 0.03$, $P = 0.881$). Examination of the data revealed no suggestive patterns for particular pest species in the spring, with the exception of spotted cucumber beetle on cucumber (below). Because our focus was on biocontrol, we examined only major pests of the crops that we planted, although other arthropod herbivores were present in the samples.

Carabids and lycosids had no indirect effects on vegetable production in the spring gardens (Table 1).

In the summer gardens, overall herbivore density on squash was marginally lower (Fig. 3D; $F_{1,3} = 8.92$, $P = 0.058$) where carabid and lycosid immigration was allowed. The presence of carabids and lycosids significantly increased squash productivity (Fig. 4; $F_{1,3} = 28.82$, $P = 0.012$). Neither pest numbers (Fig. 3D; $F_{1,3} = 5.84$, $P = 0.094$) nor plant productivity (Fig. 4; $F_{1,3} = 0.10$, $P = 0.776$) differed between 1X and 2X gardens.

Because increasing the immigration rate of carabids and lycosids into the summer plots increased squash productivity, we examined pest and foliage predator numbers by taxa on cucurbits [numbers on cucumber (spring) and squash (summer) pooled] to determine which particular taxa were affected. We pooled the spring and summer samples because the pest and predator communities of cucurbits were present in both crops, so that the arthropod communities on these crops were continuous through both cropping cycles. Nabid bugs and nonlycosid spiders were the most abundant foliar predator taxa on cucurbits in both gardens, together representing 61% of total catch. Nabid bugs were significantly lower in plots where carabid and lycosid immigration was allowed (Table 2A; $F_{1,3} = 22.42$, $P = 0.018$). Lycosids and carabids did not affect densities of nonlycosid spiders in the foliage (Table 2A; $F_{1,3} = 0.011$, $P = 0.922$). Doubling the immigration rate of the ground predators did not increase the magnitude of their effect on nabid bugs (Table 2A; $F_{1,3} = 0.09$, $P = 0.780$), but foliage spider densities were higher in 1X than 2X plots (Table 2A; $F_{1,3} = 19.04$, $P = 0.022$).

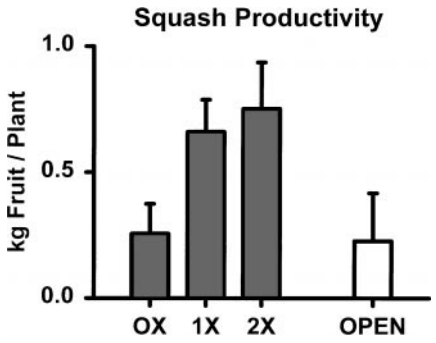

FIG. 4. Productivity of squash, the only vegetable planted in the summer gardens.

Numbers of spotted cucumber beetles on cucurbits were significantly lower in the presence of carabids and lycosids (Table 2B; $F_{1,3} = 32.21$, $P = 0.011$), whereas neither squash bug nor striped cucumber beetle densities differed between plots with and without ground predators (Table 2B; for squash bugs $F_{1,3} = 2.10$, $P = 0.243$; for striped cucumber beetles $F_{1,3} = 0.001$, $P = 0.974$). Doubling the immigration rate of carabids and lycosids never significantly increased their impact on these herbivores (Table 2B; $F_{1,3} = 4.78$, $P = 0.116$; $F_{1,3} = 2.41$, $P = 0.219$; $F_{1,3} = 3.02$, $P = 0.181$ for spotted cucumber beetles, squash bugs, and striped cucumber beetles, respectively).

Accuracy in Reproducing Open-Field Conditions

Adult lycosid activity-densities, lycosid spiderling numbers, and numbers of nonlycosid spiders sampled in the mulch did not significantly differ between 1X and OPEN reference plots (Figs. 2B–2D; $P > 0.687$). However, carabid activity-densities were significantly higher in 1X than OPEN plots, apparently due to a late-season

TABLE 1

Vegetable Production (kg/Plant; Mean ± SE) in the Spring Gardens

	Treatment			
Vegetable	0×	1×	2×	OPEN
Cabbage	0.54 ± 0.05	0.73 ± 0.09	0.54 ± 0.09	0.63 ± 0.14
Bean	2.31 ± 0.18	2.04 ± 0.27	2.04 ± 0.14	2.00 ± 0.23
Eggplant	0.41 ± 0.14	0.14 ± 0.05	0.36 ± 0.14	0.00 ± 0.00
Cucumber	0.59 ± 0.09	0.45 ± 0.14	0.54 ± 0.14	0.45 ± 0.09

Note. Allowing carabid and lycosid immigration, and doubling the immigration rate of these predators, never significantly increased vegetable productivity in the spring gardens ($P > 0.15$ for all comparisons).

TABLE 2

Arthropod Numbers (No./Plant; Mean ± SE) on Cucurbits

	Treatment			
Arthropod category	0×	1×	2×	OPEN
(A) Predators				
Nabid Bugs	0.23 ± 0.02	0.09 ± 0.03	0.10 ± 0.03	0.08 ± 0.02
Nonlycosid Spiders	0.23 ± 0.06	0.24 ± 0.03	0.20 ± 0.03	0.13 ± 0.04
(B) Pests				
D. u. howardi	0.40 ± 0.04	0.15 ± 0.03	0.19 ± 0.03	0.17 ± 0.05
A. vittata	0.58 ± 0.14	1.00 ± 0.61	0.58 ± 0.25	0.40 ± 0.18
A. tristis	2.88 ± 1.13	0.62 ± 0.25	2.31 ± 1.26	0.71 ± 0.43

Note. Densities are the mean of two sample dates, one at cucumber harvest, the other at squash harvest.

divergence between the two treatments (Fig. 2A; $F_{1,3} = 16.63$, $P = 0.027$). Foliage predator densities were similar in 1X and OPEN plots in both spring and summer (Figs. 3A and 3B; $P > 0.134$). Herbivore densities were significantly lower in OPEN than in fenced plots in the spring (Fig. 3C; $F_{1,3} = 10.58$, $P = 0.047$), an effect that may have largely been due to a difference in flea beetle numbers (flea beetle densities averaged 94 ± 2/plant in fenced plots, but 35 ± 22/plant in open plots). Herbivores on squash foliage were similar in fenced and open plots (Fig. 3D; $F_{1,3} = 0.13$, $P = 0.741$).

Productivity of cabbage, bean, and cucumber in the spring, and squash in the summer, did not differ between 1X and open plots (Table 1 and Fig. 4; $P > 0.22$). Eggplant in open plots did not produce any fruit, and thus no statistical comparison is needed.

Laboratory Feeding Trials

Intraguild predation occurred between carabid species, between lycosid genera, between lycosids and carabids, and among carabids and lycosids and the other ground predators that we tested (Fig. 5A). Lycosids were intrageneric predators; strict cannibalism could not be detected because lycosids were identified only to genus. Carabids were never cannibalistic. Predation was generally size determined, with larger predators eating smaller ones.

Scarites spp. and *E. sodalis* consumed all stages of the three cucurbit pests (Fig. 5B). *H. pennsylvanicus* regularly consumed only smaller, immobile pest stages (i.e., squash bug eggs). *Hogna* spp. consumed all mobile stages of cucurbit pests, although they never consumed eggs (Fig. 5B). *Pardosa* spp. preyed upon squash bug nymphs, but like *Hogna* spp., they ignored squash bug eggs (Fig. 5B).

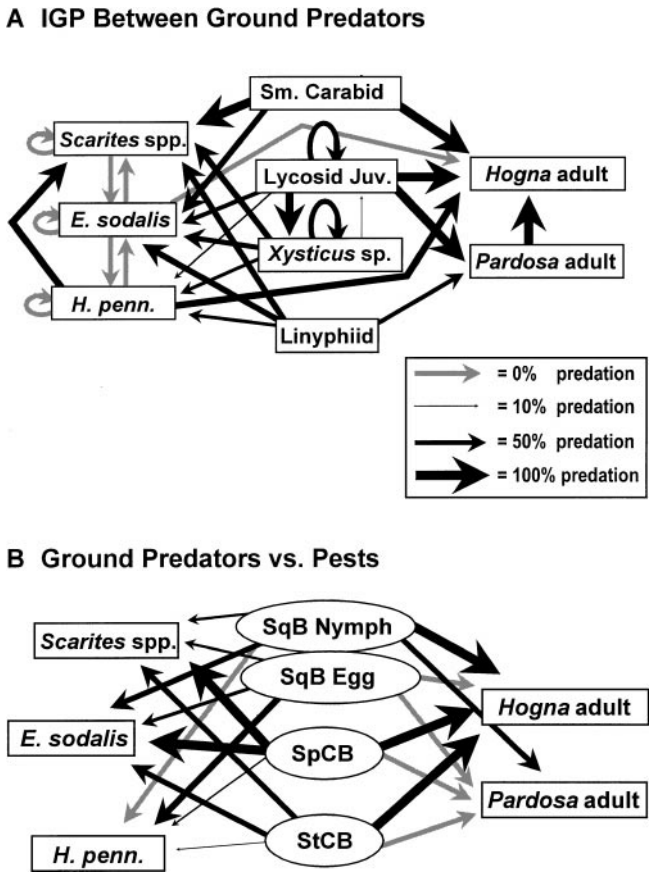

FIG. 5. (A) Web of intraguild predation between ground predators as measured in laboratory feeding trials. Predators were housed together for 7 days; predation is reported as the total percentage over this period. *Scarites* spp., *E. sodalis*, and *H. pennsylvanicus*, the three most abundant carabids at our field site, are relatively large carabids (*ca.* 1.5 cm). *Hogna* are relatively large wolf spiders (body length >1 cm for adults); *Pardosa* are smaller (*ca.* 0.5 cm body length). Lycosid juveniles could not be reliably identified to genus and so are presented separately from adult lycosids. Small carabids were several species of carabids less than 1 cm in length. Linyphiids and *Xysticus* sp. are two common nonlycosid ground spiders. Pairings of carabids with one another, and with other ground predators, were replicated 15–20×; lycosid pairings were replicated 5–10×. Arrows denote energy flow, i.e., point from victim to predator. Line thickness is scaled to represent the relative frequency with which predation was observed. Gray arrows are pairings in which predation never occurred; absence of an arrow indicates that particular pairing was not done. For each pairing, equal numbers of predators were maintained singly as a control; none of these animals died. (B) Predation by ground predators on cucurbit pests. Web constructed as described above. Predators were housed with pests for 3 days. Pairings of carabids and lycosids with cucumber beetles were replicated 16–26× and 9–13×, respectively. Pairings of predators with squash bug eggs and nymphs were replicated 6–10×. For each pairing, equal numbers of pests were maintained singly as a control; none of these animals died.

DISCUSSION

Carabids and lycosids responded differently to our experimental doubling of the ground guild's immigration rate. Carabid numbers approximately doubled, whereas lycosids did not increase. Thus, predator interference at most only weakly affected carabid densities. Intraguild predation between adult carabids has been infrequently reported in the literature, although the larvae can be cannibalistic (Currie *et al.*, 1996; Thiele, 1977). In contrast, among lycosids, cannibalism and intraguild predation appear to be more common (e.g., Oraze and Grigarick, 1989; Wagner and Wise, 1996, 1997). In our experiment we cannot differentiate between carabid predation on lycosids and intergeneric and interspecific interference between lycosid species, since both carabids and lycosids were manipulated simultaneously. Further study is needed to differentiate between these processes as regulators of lycosid densities in this system.

Antipredator behaviors can have community impacts that mimic the direct effects of predation on mortality (Wissinger and McGrady, 1993). For example, Moran and Hurd (1994) recorded increased emigration rates of spiders in response to increased density of mantid predators. In our experiment lycosid spiderlings could

have increased their ballooning rate in response to increased predator density, in part explaining the convergence in lycosid spiderling densities. However, cannibalism among young lycosid spiderlings may be substantial (Wagner and Wise, 1996), and adult lycosids are too large to balloon (Crawford *et al.*, 1995) and could not climb our fence barriers; thus, intraguild predation and cannibalism likely played a major role in causing the convergence in lycosid densities.

The laboratory feeding studies provide some insight into important interactions in the field, although comparisons between simplified microcosm studies and field studies should always be made cautiously. In the feeding trials none of the three most abundant carabid species was cannibalistic, and interspecific predation between carabids was rare. *Scarites* spp. did prey upon *H. pennsylvanicus*, but since these species have peaks of activity at different times in the season (Barney and Pass, 1986b), such interactions are rare in the field. Furthermore, lycosids rarely preyed upon carabids, probably because their hard elytra and relatively large size made them unattractive prey for the spiders. These results suggest that interactions between carabids, and between carabids and lycosids, should not limit carabid densities, which is consistent with the results of our field experiment. For lycosids, both inter- and intrageneric predation were common, as probably was cannibalism (although we did not identify trial animals to species). The carabids *Scarites* spp. and *E. sodalis* both preyed upon lycosids. Thus, these laboratory feeding trials were also consistent with the field results: unlike carabids, lycosids are frequent victims of intraguild predation and probably cannibalism.

Several studies have examined hedgerow or field-edge characteristics that help conserve carabid and spider populations (Best *et al.*, 1981; Gravesen and Toft, 1987; Nentwig, 1988; Luff and Rushton, 1989; Mangan and Byers, 1989; Heidger and Nentwig, 1989; Hance *et al.*, 1990; Bedford and Usher, 1994; Kajak and Lukasiewicz, 1994; Barbosa, 1998), which could in turn increase movement from these habitats into nearby agricultural fields. Our field experiment suggests that this approach may be most successful in increasing densities of carabids, which appear to exhibit little *in situ* self regulation once they immigrate into agricultural fields. For lycosids, it may be just as important to manipulate in-field habitat structure to increase their numbers, since they are strongly limited by in-field predator interference. The results of in-field habitat manipulation can be dramatic. For example, Riechert and Bishop (1990) increased spider densities 10-fold by adding straw mulch to vegetable gardens.

Predator interference did not occur only within the predator guild that we manipulated. Carabids and lycosids reduced nonlycosid spiders by 50%, and foliar predator densities in the summer crop were lower where carabid and lycosid immigration was allowed, mainly due to a reduction in nabid bugs. It is perhaps not surprising that lycosids and carabids could negatively impact other predators of the ground layer, which they should frequently encounter, but the reduction in nabids is more unexpected. However, differentiating between carabids and lycosids as ground predators, and nabids as foliar predators, probably over simplifies actual foraging behaviors. Both lycosids and carabids occasionally forage in plant foliage (Barney and Pass, 1986a; Snyder and Wise, *pers. obs.*), and nabids forage on the ground surface (Lattin, 1989).

Biocontrol Effectiveness of Carabids and Lycosids

Predators and productivity were not affected by our manipulations of carabid and lycosid immigration in the spring garden. Bean had very low pest densities, and productivity was high in all treatments, whereas both cabbage and eggplant were attacked by large numbers of a single pest (imported cabbage worm on cabbage and flea beetle on eggplant). The majority of bean and eggplant foliage is above the ground, where any pests may be out of reach to ground predators through most of the growing season. In contrast to our findings, Riechert and Bishop (1990) found reduced damage to cabbage where spider densities were higher. Clearly, more studies are required to determine if, and when, generalist predators can be effective biocontrol agents on bean, cabbage, and eggplant.

On cucurbits, carabids and lycosids depressed numbers of spotted cucumber beetles, but striped cucumber beetles and squash bugs did not show statistically significant decreases. Lycosids in the genus *Hogna* and the carabids *Scarites* spp. and *E. sodalis* fed upon cucumber beetles in the laboratory feeding studies. Any of these predators could have contributed to the reduction in spotted cucumber beetles observed in the field experiment. The reduction in spotted cucumber beetles was apparent in spring on cucumber and continued through squash harvest, but only squash productivity increased, suggesting that the impact of ground predators on cucumber beetles is slow to develop. Because our first spring-garden foliage sample was not until harvest, we do not know if spotted cucumber beetle numbers were reduced earlier in cucumber growth. It is also possible that cucumbers may be more resistant than squash to cucumber beetle feeding. As an additional complication, by the end of the season, carabid densities in the 1X plots exceeded those in the open reference plots. Thus the impact of our predator manipulation on herbivores, predators, and productivity in the summer gardens might in part reflect particularly high densities of carabids in the fenced plots at the end of the season. Lycosid densities, however, were practically identical in open reference and 1X plots.

Herbivore densities, densities of predators other

than carabids, and plant productivity did not differ between 1X and 2X treatments, except for nonlycosid spiders on cucurbit foliage. Interpreting the paucity of significant differences between 1X and 2X treatments is difficult because only carabids were more numerous in the 2X treatment. This could mean that of the predators that we directly manipulated, only lycosids exert significant regulation of other arthropods because elevated carabid numbers did not increase the magnitude of arthropod or plant responses. Alternatively, nonlethal (i.e., behavioral) interference between carabids, and between carabids and lycosids, may have increased in the 2X treatment, leading to a reduction in per-capita predator impact. Further experiments, in which carabids and lycosids are manipulated separately, would increase our understanding of the relative impact of each taxon on each other, on cucurbit pests, and on cucurbit production.

Future Research

Our study provides evidence that carabids and lycosids can exert sufficient biocontrol in squash to increase fruit production, which is an economically important measure of productivity. We uncovered predator interference within the guild of generalist ground predators that we manipulated, and between this guild and other predators on the ground and in the foliage. Predator interference was common and did not preclude biocontrol effectiveness, but neither were carabids and lycosids consistently successful biocontrol agents. Our experiments suggest several directions for future research. First, more research is needed on the relative roles of carabids and lycosids in producing the patterns that we uncovered. Second, the quantitative impact of this complex of generalist ground predators on vegetable pests and production warrants closer examination. We found only limited evidence of their effectiveness, with cucurbit crops appearing to be the most likely candidate for effective biocontrol of the crops that we planted. Experiments with cucurbit monocultures in which carabid and lycosid densities are manipulated separately and in combination, and in which pest sampling is more intensive, would clarify further the potential value of conserving and enhancing densities of these generalist predators as a biocontrol strategy in vegetable production.

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